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CONTRIBUTION TO THE KNOWLEDGE OF THE NUDIBRANCHIATE MOLLUSK, MELIBE LEONINA (GOULD)*

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INTRODUCTION

THE writer's attention was drawn to this rather unusual type of molluskan life (*Melibe leonina*) in observing the living animals at the Puget Sound Biological Station, located at Friday Harbor, Washington, during the summer of 1914, and inasmuch as little was known concerning the species, an effort was made to assemble such data as might be of interest relative to its habits and development. The results of this study are presented in the following pages.

It was originally intended to publish these in connection with work on the morphology of the species, now under preparation, but owing to the extent of the morphological data and the crowded condition of the morphological journals it seems best to have this other matter appear separately.

TAXONOMY

The genus *Melibe* (Rang), together with *Tethys* (Linné), constitutes the family *Tethymelibidæ,* which forms one of the numerous groups of family rank included in the sub-order *Nudibranchiata* of the opisthobranchiate *Mollusca.* The type of the genus *Melibe* was discovered at the Cape of Good Hope and described by Rang in 1829. Since that time eleven species have been added by various

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[1] In my previous writings, *Biol. Bull.,* Vol. 35, No. 4, 1918; *School and Society,* Vol. 9, No. 232, 1919; Pub. Puget Sound Biol Sta., 2, No. 49, 1919; AMERICAN NATURALIST, Vol. 54, 1920, my name is written Kjerskog- . . . which is the modern form of the original (Kjerschow) substituted henceforth.

authors. Gould, 1852, described *Melibe leonina,* the species upon which this paper is based, from Puget Sound, founding for it the genus *Chiorœra* now merged in *Melibe.* Bergh, in a series of papers between 1863 and 1907 revolutionized the classification of the *Nudibranchiata.* He divided the nudibranchs into two sections: the *Kladohepatica* and *Holohepatica porostomata.* Although his work was primarily systematic, it was based on morphological studies. He added six species to the genus *Melibe,* including *M. pellucida,* from the coast of Washington near the mouth of the Columbia River. His description indicates such a close similarity to *M. leonina* that it may be questioned whether this species is entitled to specific rank; material from the type locality may be necessary to settle this point. The more recent work on taxonomy by Sir Charles Eliot, 1910, modifies Bergh's work to some extent.

No detailed study has been made of *M. leonina* previous to the present work and our knowledge of the species rested largely with the brief description and figure presented by Gould.

DISTRIBUTION

Melibe, as far as known, is restricted to the Pacific and Indian Oceans, and to the South Seas. On the eastern

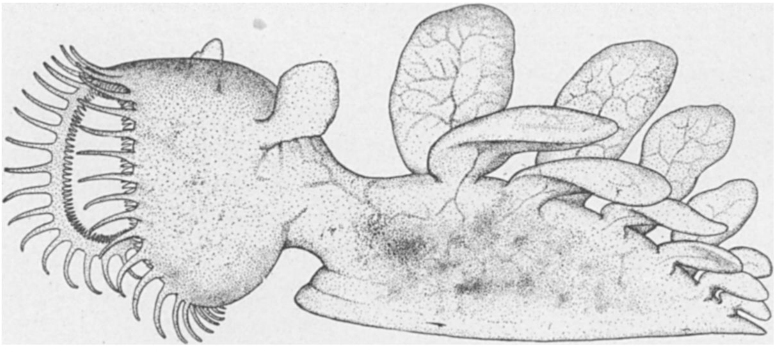

FIG. 1. *Melibe (Chioracra) leonina* Gould. From a drawing by Mr. Bert Elliot, private artist to Professor Trevor Kincaid, University of Washington. Slightly changed. × 1/3.

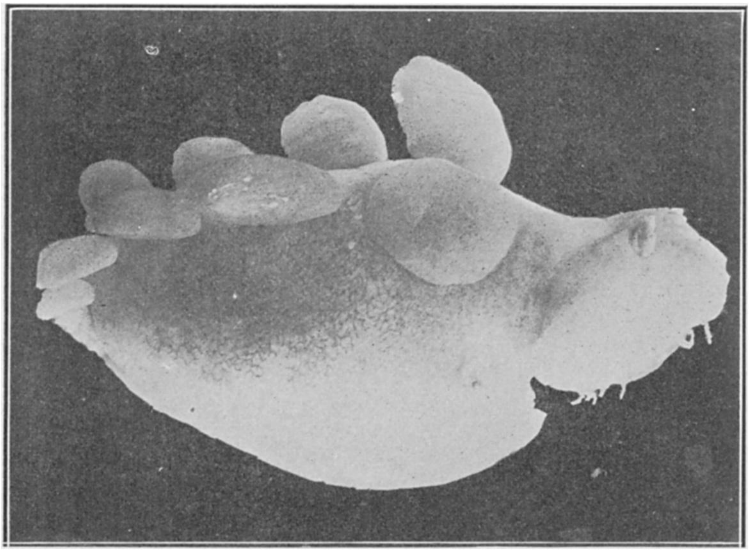

Fig. 2. Photograph, by author, of preserved specimen of *M. leonina* showing profuse branching of hepatic system in the body-wall; the hood is contracted into a knob as when the animal swallows. Slightly reduced.

side of the Pacific, two species have been described, *M. leonina* Gould, 1852, and *M. pellucida* Bergh, 1904. On the western side of the Pacific, various species have been found by Bergh from the Japanese Island to the Straits Settlements. One species has been described by Angas, 1864, from Australia; one from the Pacific by De Filippi, 1868; one from the Sandwich Islands by Pease, 1860; and several species from the Indian Ocean by Rang, 1829, Alder and Hancock, 1864, and Eliot, 1902. So far no species of this genus seems to have been found on the coasts of the Atlantic Ocean. In these parts of the world, and in the Mediterranean and Caribbean Seas, it seems, according to works of Bergh, 1877, 1890*a*, Locard, 1885, Viguier, 1898, and Eliot, 1910, to be replaced by *Tethys* Linné. Eliot 1910 (pp. 12–13), fails to record *Melibe* among the American Pacific fauna. Neither *Tethys* nor *Melibe* seems to occur in the northern waters. All the Melibidæ recorded by Agassiz, 1852, G. O. Sars, 1878, Johnston, 1838 (*Melibea*), are, in fact, not *Melibe*, but

Doto. Von Marten's (1879) *Melibea* does not seem to come under either type, although from this author's description certain characteristics are in common with that of *Melibe.* For some time there was considerable confusion in regard to these genera. Bergh, 1863, and again in 1871, makes this clear when he writes:

> Das Geschlecht Doto wurde von Oken (1815) auf der Gemlin'schen *Doris coronata* (Bomme) aufgestellt. Jahre nachher (1829) bildete Rang (Man., p. 129, pl. 3, f. 3) eine neue Geschlechtsform Melibe ab, dessen Typus eine Nacktschnecke war, die er im Meere des Vorgebirges der guten Hoffnung (Cap) am schwimmenden Meeresgrase fand. Das Rang'sche Geschlecht, das von späteren Verfassern gewöhnlich Melibaea genannt ist, ist am meisten mit dem Oken'schen Doto identificirt worden, in der Art, dass alle bisher bekannten Melibaeen—eben mit Ausnahme der "Melibe" rosea von Rang—der Doto-Gruppe gehören. Die Melibaea, autt. sind in der That mit den Doto'en identisch und mussen diesen Namen bekommen. Die Meliben Rangs dagegen werden, wie früher von mir hervorgehoben (Schiödte Naturh. Tidskr., 3 R, I, 3, 1863, p. 480), einen ganz verschiedenen Geschlechstypus bilden, den ich als mit den Chioraeren von Gould verwändt betrachtete, der aber einer späteren Mittheilung von Alder und Hancock (1864) zufolge den Scyllaeen näher (?) käme.

The genus *Tethys* Linné, 1758, the nearest relative of *Melibe* Rang, 1829, was also confused with other forms, *e.g., Aplysia.* Pilsbry, 1895, has, however, cleared up this point. He shows that the various specific names attached to *Tethys,* such as *fimbria, fimbriata,* and *leporina,* are to be considered synonyms. Bergh, 1880*a*, and Krause, 1885, do not record *Melibe* in their nudibranchiate collections from the north Pacific. Likewise, investigators in the north Atlantic, on both sides of the ocean, including a number of explorers and independent workers such as Alder and Hancock, 1842 and 1845; Meyer and Möbius, 1865; M. Sars, 1870; Aurivillius, 1885; Garstang, 1890; Krause, 1895; Ohdner, 1907; Walton, 1907; Théel, 1908; and Johnson, 1915, do not record *Tethys* or *Melibe* in their collections. These species are, therefore, restricted to the warmer seas.

When the Puget Sound Biological Station[1] was estab-

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[2] This station was first known as the Puget Sound Marine Station; its founder, Professor Trevor Kincaid, remained its director until 1914.

lished in the San Juan Archipelago in 1904, it was found that *Melibe leonina* was not uncommon in the vicinity, although like many pelagic organisms its abundance was subject to great fluctuations. In the summer of 1912 it was particularly abundant, great numbers appearing among the fronds of *Nereocystis* drifting past the floating dock in front of the station. At this time Prof. H. L. Osterud, of the University of Washington, gathered and preserved a considerable number of specimens. The largest specimen obtained was six cm. in length, the time of collecting being the latter part of July. During the season of 1913 very few were seen. In 1914, the writer found several specimens of large size, 8 to 13 cm. in length. These were taken among the floating eel-grass, *Zostera marina*. In the summer of 1915 only two specimens were found. It appears that the genus *Tethys* is of spasmodic recurrence in the Mediterranean (Viguier, 1898). The appearance of *Melibe* does not seem to be determined by any particular season, as Prof. Osterud found specimens spawning when visiting the Biological Station early in March of 1916. The period of existence of this nudibranch must be more than one year, or one season, judged from the sexual condition in this species which has shown maturity in individuals ranging in size from two to fourteen centimeters. Alder and Hancock (1845), p. 24, think the period of existence for a large number of species "not much exceeding one year."

ECOLOGY

There is a striking similarity between the *Kladohepaticæ*, not only between the members of any given family, but also between members of different families within the section. The former is well illustrated by *Tethys* and *Melibe*, members of the family Tethymelibidæ. This similarity is not only morphological, but equally true as to manner of living and general behavior, for instance, the method of swimming. *M. leonina* may crawl on the leaves of the eel-grass; or it may float with the back up, the hood having air under it, or the papillæ serving as floats. In the latter case *Melibe* alternately bends laterally the anterior end to angles of 45 degrees. During these alternating bendings of the body the movements are swiftest when the body is relaxed from the 45-degree bend. By this method it conveys itself slowly through the water. However, on the surface tension of the water or on the eel-grass, the movements are caused by the ciliary action of the ventral surface of the foot, because progressive movements occur without visible bodily contortion. *Tethys leporina* Linn. moves through the water by similar means (Bergh, 1877 and 1883). In its case, however, the large veil, as well as the lateral bendings of the body, plays an important part. Gould, 1852, in his original description of *Melibe leonina*, says:

> This animal swims by lateral flexions of the body, the foot being then folded; and when crawling it is able to flex its enormous head laterally with considerable force (p. 310).

Scyllæa pelagica Collingwood, 1879, swims very much like *M. leonina* and *T. fimbria;* and Garstang, 1890, mentions that *Lomanotus* Vérany, swims "vigorously through the water in the dish . . . by lashing the body from side to side." But neither Gould, Bergh, Collingwood, nor Garstang mentions ciliary action as a factor in locomotion.

Collingwood, 1879, says in part:

> Considerable numbers of this pelagic species were found upon *Sargassum bacciferum,* floating in Lat. 25 N., Long. 37 W., most species of weed having one or more specimens. The animals were in constant movements of contracting and writhing. In the water they swam freely, moving the head and tail from side to side alternatingly, so as nearly to touch one another; and when thus swimming were always, owing to the weight of the papillary prolongations and tentacles, back downward, and bore grotesque resemblance to a four-legged animal with ears, such as a Skye terrier.

Another similarity between *Scyllæa* and *M. leonina* is the manner of dropping from the surface to deeper water. In the case of *leonina* this is a sort of death feigning. *S. pelagica* may be found at the surface or in deeper water. Collingwood mentions it as assuming certain aspects when it falls through the water to a considerable depth, where it is frequently found. *M. leonina* possesses the same habit. In so doing the muscles of *leonina* are absolutely relaxed and the animal appears dead. The means by which the animal gets to the surface are not known, unless it be by its general mode of swimming. One striking difference between these two forms is: *M. leonina* may swim with the back upward, "the weight of the papillary prolongations," important in *S. pelagica,* being apparently of no account.

The eel-grass offers an excellent feeding ground for *Melibe.* Here the water must not only be calm, but may abound in small Crustacea. *Zostera,* which grows in large beds in the bays near the Biological Station at Friday Harbor, offers also a suitable assembling place for *Melibe* where it may pair and lay its eggs. At low-tide the eel-grass floats on the surface of the water and leaves many inclosures of open water. In these open spaces *M. leonina* collect and copulate, as was observed in the summer of 1914. In such spaces, as described, a considerable number of *Melibe* had collected, and some of them were copulating, being united head to head, the foot of one mate facing the surface. The excellent condition of the water offered an ample opportunity to study the mode of swimming and the manner of feeding. The former has partly been described above, and will further be discussed under the topic on observations in the laboratory; the latter corresponds to Eliot's description (1902) of *M. fimbriata* Ald. and Hanc. *M. leonina* is not so definite in its movements during its feeding as is *M. fimbriata,* yet some similar method of feeding is pursued. Both species have a large hood. In the case of *leonina* the hood is extended very widely (Fig. 1), when the animal is searching for food, and is periodically contracted into a knob (Fig. 2), when food is obtained. When the hood is open, *leonina* tosses it sideways, holding it in direct position for the capture of small horizontally swimming crustaceans. Eliot, 1902, says of *M. fimbriata:*

> In spite of its want of jaws, *Melibe fimbriata* is a most voracious animal, and I more than once found in the stomach which I examined limbs of Crustacea more than an inch long. . . . The movements of the animal are rapid and energetic, whether it crawls or swims. It can float on the surface, foot uppermost (p. 70).

Melibe leonina is actively predaceous also; its gizzard has been found completely filled (Agersborg, 1919) with minute Copepoda, Amphipoda, and larger and smaller Isopoda, until the gizzard would bulge out into almost a perfect sphere; ordinarily the gizzard has only a partial enlargement; its normal size is a little larger than that of the proventriculus, and the anterior part of the intestine.

Daugherty and Daugherty, 1912 and 1917 (p. 83), refer to nudibranchs as vegetable feeders; having mentioned *Eolis* and *Pleurophyllida,* they say:

> These soft naked sea-slugs live in shallow water near the shore, crawling about and feeding upon the sea-weeds.

However, only a few of the rarer species are phytivorous; the majority are carnivorous, a fact which is recognized by the authorities on nudibranchiate *Mollusca.* Thus Bergh, in most of his descriptions of nudibranchiate fauna, reports in favor of animal diet: 1880*a* (*Akiodoris lutescens*) p. 56, (*Lamellidoris bilamellata*) p. 64, (*L. luptricina,Acanthodoris pilosa*) p. 101,(*Triopha modesta*) p. 116; the food of these forms consisted of "indeterminable animal matter, mixed with some diatomaceæ, . . . and with some Polytholamia, . . . with larger and smaller pieces of small Crustacea, . . . and a little indeterminable worm, of the length of 2.0 mm., . . . spongiary masses and different Radiolariæ of a diameter of 0.09 mm." In regard to *Tritonia reticulata,* the same author, 1881, says:

> Die Tritoniaden sind Raubthieren und scheinen sich hauptsachlich von Alcyonien und ähnlichen Thierformen zu ernähren.

Again, 1883, referring to *Tethys leporina,* he says:

> Tethys ist ein Raubthier und sein Nahrung besteht namentlich aus kleinen Ophiuren, deren Reste oft ganz den Magen erfüllen.

1890*a*:

> Der Magen und der Darmen von Nahrung vollgeslofft; dieselbe bestand aus Massen von kleinen Decapoden, mit Bruchstücken von kleineren Gasteropod Schalen und Sandkörnern vermischt (p. 158).

1894 (*Dendronotus robustus*):

> In der verdauungshöle unbestimmbare thierische Masse, mit Diatomeen vermischt (p. 144).

And finally, describing the food of *Melibe rosea*, 1907, he says:

> The contents of the alimentary cavity (specimen 1.5 cm.–3.8 cm.) were animal matter with remains of small Hydroids (p. 98).

Alder and Hancock, 1845, p. 23, say:

> But, though so patient and long-suffering in the endurance of hunger, these little animals are very voracious. The greater number of them are carnivorous; living principally upon zoophytes and sponges. The *Alcyonium digitatum* is a favorite food with the *Tritoniæ;* and the *Actiniæ* and *Lucenariæ* often fall prey to the attacks of the *Eolides*. These latter, indeed, do not scruple occasionally to devour the weaker among their own brethren, as we have recorded elsewhere. Sir J. G. Dalyell states that his *Eolis histrix* (Drummondi) 'fed voraciously on mussel, and on common periwinkle, whereof large portions were swallowed entire'; and he thinks that *Goniodoris nodosa* feeds upon *Ascidia papilla* (*Cynthia rustica*), to which he attributes the reddish colour observed in the viscera. This colour, however, is caused by the liver and ovary. We have taken from the stomach of *Eolis papillosa* minute specimens of the common mussel, and a small *Terebra* from that of Tethys. The more common food of the tribe, however, is the flexible zoophytes. Until lately the Dorides have been considered vegetable feeders, but this would appear not to be the case. *Doris tuberculata* feeds upon common encrusting sponges (*Halichondria panicea*), and sponges and zoophytes seem to constitute the food of most of the others. A few of the gregarious Nudibranchs, such as *Polycera quadrilineata, Hermæa dendritica,* and *Alderia modesta,* which congregate on marine algae, appear to be phytivorous; but *Eolis despecta,* and *E. exigua* though not unfrequently gregarious on the fronds of *Laminaria digitata,* are only found on those parts of the plants that are covered with the parasitic zoophytes, *Laomedea geniculata* and *L. gelatinosa,* on which they feed and deposit their spawn.

Meyer and Möbius, 1865, are of the opinion that it is rather difficult to determine whether Nudibranchs are carnivorous or phytivorous, that is, that the food of Nudibranchs is very variable. In part they say of *Elysia viridis* Montagu, p. 10:

> Sie nährt sich wahrscheinlich von Pflanzen.

Page 23:

> *Eolis alba* frisst, wie die anderen Kieler Arten ihrer Gattung, thierische Stoffe.

Page 31 (*Eolis papillosa*):

> Ihre Nahrung sind Thierstoffe; besonders liebt sie Actinien. Kleinere Exemplare der *Actinia plumosa* greift sie am Fussrande an, und frisst ein halbmondförmiges Loch hinein, das sie immer mehr vergrössert.

This is also the opinion of Hecht, 1895, p. 621:

> Il n'est donc pas possible d'établir à ce point de vue une division bien tranchée. On peut dire seulement, que les familles les plus franchement herbivores sont les Hermaeidae et les Elysiidae, et en général les Ascoglosses qui, comme Ihering et d'autres l'ont remarqué, ont une masse buccale disposée pour exercer une succion. . . .

Page 622:

> Les Eolidiens sont tous franchement carnivores et présentent, parmi les grandes espèces, quelques types d'une voracité extraordinaire. *Eolis coronata* . . . devore des *Elysia viridis;* à l'autopsie j'ai trouvé des radulas dans son tube digestif. Les petites espèces *Eolis despecta, E. exiqua, E. olivacea* peu faites pour de grands déplacements, vivent à demeure, comme je l'ai dit plus haut, sur des colonies d'Hydroides.

Page 223:

> *Calma glaucoïdes,* qui, pendant une période de sa vie tout ou moins, se nourrit, je l'ai dit, d'embryons de Poissons. Le régime des Doridiens est moins uniforme; certains genres sont probablement herbivores. Plusieurs espèces de Doris se nourrissent d'Eponges calcaires dont on retrouve les spicules dans les excreta. . . . Plusieurs espèces de Goniodoris se nourissent de Bryozoaires. Il est probable que *Polycera quadrilineata* mange des Algues. Il faut signaler ici les observations de Prouho, sur la façon particulière dont *Idalia elegans* se nourrit de certaines Ascidies. Quant aux Ascoglosses, j'ai indiqué plus haut que *Hermaea dentritica* dévore les couches superficielles des Codium tomentosum, qu'elle réduit à l'état d'un petit moignon verdâtre. *Elysia viridis* se nourrit aussi de Codium tomentosum, mais sans marquer de préférence pour telle ou telle région; j'ai du reste observé qu'elle s'accommode aussi d'autres Algues.

Jeffreys, 1869, contributes to this subject and says:

> Although most of the order are zoophagous, *Limapontia* and others of a simpler kind feed on seaweeds.

And von Ihering, 1876, p. 37, referring to *Tethys* states:

> Das der Magen eines so gefrässigen, jeder Bewaffnung des Mundes baaren Raubthieres wie *Tethys* eines solchen Schutzes ganz besonders bedarf, wird sofort verständlich, wenn man den Mageninhalt desselben kennen lernt. Ich fand denselben ausser aus Tangstücken bestehen in zahlreichen Crustaceen, kleinen Echinodermen und mehrmals auch kleinen Fischen, von denen einer 4 cm. lang war. Dasselbe Thier enthielt noch die Otalithen eines andren Fisches, welche diejenigen des ebenbezeichneten um das Doppelte übertrafen.

Melibe fimbriata Ald. and Hanc., is, according to Eliot, 1902,

> in spite of its want of jaws, a most voracious animal.

This same author says he more than once found in the stomach he examined limbs of Crustacea more than an inch long. And, in 1910:

> Thus the red British Dorids *Rostanza coccinea* and *D. flammea* eat red sponges, such as *Microciona atrasanguinea* (p. 5).

In fact, this author thinks that most Dorids feed on sponges (Eliot, 1910, p. 39). Step, 1901, referring to the crowned sea-nymph, *Doto coronata,* says it feeds upon Hydroids (*Sertularia* and *Plumularia*) and Corrallines (*Antennularia antennina*). The marble slug, *Lomanotus marmoratus,* feeds upon corrallines which it closely resembles in color and ornamentation. Eolis feeds upon anemones, *Sagertia, Lucernaria;* Sea-mats, *Tubularia,* various sponges and *Obelia.* The crimson Hermæa (Ascoglossa), *Hermæa bifida,* feeds on small crimson weeds (*Bryopsis, Codium, Enteromorpha* and *Ulva*). Vayssiere, 1901, p. 84, referring to *Tethys fimbria,* Bohascht, Delle Chiaje (Synon. *T. leporina* Linné, Cuvier), writes:

> Dans l'intérieur du premier renflement stomacal (jabot), je trouvais d'ordinaire une grande quantité de filaments fibreux de Zostères; ces mollusques doivent en aspirant avec leur trompe, absorber des débris de

ces végétaux et dissocier leurs fibres par les contractions répétées des parois musculaires de cette poche.

Page 85:

> Au milieu de ces débris, ils trouvent de petits crustacés (*Entomostracés, Amphipodes, Isopodes,* jeunes *Décapodes brachyures*) et autres petits Invertébrés, circulant parmi les Zostères, qui doivent former la base de leur nourriture.

Thus it is seen that even the carnivorous *Tethys* may be phytivorous. Vayssiere, 1911, p. 43, says of *Halgerda willeyi* C. Eliot, 1903:

> La poche stomacale était remplie de gros débris Crayeux constitués par des fragments de madrépores et de bryozoaires que ce mollusque arrache et broie avec sa forte radula.

Finally, MacFarland, 1912, p. 530, says in regard to the Dironidæ (*Diron allolineata*):

> Diatom shells and minute spicules, these made up a very small portion of the total contents.

Nudibranchs may be said to be omnivorous; as seen above, a species which is void of radula, *e.g., Tethys,* may at one time be carnivorous, at another time phytivorous; likewise forms possessing radula (*Acanthodoris*) are omnivorous. The largest number seem to be carnivorous notwithstanding; a few, the *Hermæidæ* and *Elysiidæ,* are phytivorous.

Means of Defense

Upon being first encountered, *Melibe leonina* appears brown, but when examined in the aquarium one can easily see that the brown coloring is rather superficial in comparison to the marked transparency which the body possesses. This transparency is so great that the internal organs, such as the alimentary canal, the organs of reproduction, and the heart, can be easily seen. The possibility of actually seeing these organs through the body wall is due to the arrangement of the muscles and the connective tissues, and because the body-fluid contained in the perivisceral cavity, between the visceral organs and the muscles, the connective tissues, as well as the blood, are colorless. This characteristic is also common to *M. pellucida* Bergh, 1904; and *M. vexillifera* Bergh, 1880.

Upon touching the curious-looking animal it gives off a peculiar odor. This is rather strong, and resembles that of oil of bergamot. It is caused by a secretion from small compound saccular glands lying immediately under the ectoderm (Fig. 12). These glands are distributed all over in the external parts of the body: in the body wall, the papillæ, under the ectoderm of the exterior part of the hood, and in some cases, under the ectoderm of the foot. None of these glands seem to be present under the ectoderm of the ventral side of the hood. The extent of distribution of the odoriferous glands seems to indicate that they have a definite use and purpose, *e.g.*, that of defense.

Meckelii, 1838, describes the odor exuded by *Tethys leporina* as resembling citron, or being rather pleasant. And Bergh, 1877, says:

> Von . . . toten Thiere habe ich irgend eine Spur bemerkt, dagegen einen nicht starken, etwas besonderen, aber nicht wesentlich unbehablichen Gestank.

Hecht, 1895, discusses the various means of defense possessed by Nudibranchs. He mentions protective coloration, nematocysts, mucous glands and death feigning. The last will be discussed presently; the first two may only be referred to, as *M. leonina* possesses no protective coloration, and has no nematocysts as a defensive means. It may, however, be stated that in the aquarium, *Melibe leonina* became even more transparent than it was when seen in its natural environment. This change of color was also observed by Alder and Hancock, 1845, on a number of Nudibranchs kept in captivity: "In such cases they generally lose a good deal of colour and become very transparent," and that coloration is not caused by the color of the food taken, but by the color of the liver and gonads. Eliot, 1910, says:

> The colour of Dorids is to some extent affected by their food, though less than that of Eolids. The brightly coloured species often frequent and feed on similarly bright sponges or Ascidians, and when they do not obtain their usual food in confinement they lose their colour (p. 5).

An increased transparency when kept in an aquarium, *e.g.*, a glass-jar, may be designated adaptive coloration. The odorous substance that the animal exudes when touched by an enemy is its main protection. However, Step, 1901, records some very interesting facts relative to protective coloration among Nudibranchs:

> *Dendronotus frondosus* is obviously adapted to life among sea-weeds and coralline, resembling some small red-brown sea-weeds (*Collithamnium*). It is said to be highly edible, having nothing in its flavor to displease the taste of the most fussy fish; and therefore its disguise is absolutely necessary to the species (p. 288–289).

Evidently *Melibe leonina* needs no protective coloration, having, as said above, odoriferous glands. One reason why it does not possess nematocysts is perhaps because it does not live on Hydroids, but mostly on Crustacea.

Glaser, 1903, in his discussion of the origin of nematocysts in Nudibranchs gives a historical review, including a number of citations all of which refer to the nematocysts as having been taken in with food. The food then seems to be the origin of the nematocysts in the Nudibranchs; *M. leonina*, which does not feed on hydroids, has no nematocysts in its system. The marble slug, *Lomanotus marmoratus*, according to Step, "Feeds upon Corallines which it closely resembles in colour and ornamentations"; Gamble, 1892, however, says that cnidocysts are absent.

Bergh, 1890*a*, mentions experiments by Krugenberg, 1880, who tried to determine the physico-chemical constituents of the odoriferous glands, as well as of the liver and blood of *Tethys fimbriata* (s. *leporina*), and says that *T. leporina* has a peculiar musk-like nauseous odor which it uses as a means of defense against its enemies. This is, without doubt, the office of the odor in the case of *M. leonina* also. The actual nature or constituents of the substance which causes this defensive odor have not been determined.

Another means of protection is self-mutilation, exemplified by *Discodoris fragilis,* that according to Eliot, 1899, throws off part or the whole of its mantle edge. Collingwood, 1868, also records this habit of self-mutilation of a *Doris.*

EMBRYOLOGY

The Egg-body (*Nidosome*)

Bergh, 1902, describing the egg-body of *Melibe bucephala* says:

> The spawn forms a large heap of a diameter of 3.5 cm., composed of the innumerable windings of a dull yellow tube of a diameter 0.75 mm. The tube contains inside of the tough transparent covering several series of displaced, more or less cleft eggs.

From this description it is clear that this nidosome is quite different from that of *M. leonina;* it seems, indeed, strange that the egg-body of two closely related species can differ so widely. The external features of *M. bucephala,* according to Bergh's description, are not much different from those of *M. leonina.* It may be a question whether the egg-body attributed to *M. bucephala,* by Bergh, actually belongs to this species.

The writer during the summer of 1914 found several nidosomes among the eel-grass, but it was not known to which animal they belonged until *Melibe leonina* was seen to lay the same kind in the aquarium of the laboratory (Agersborg, 1919). These nidosomes of transparent mucous, or gelatinous substance, were funnel-shaped, when suspended in the water, with the apex attached to some solid object (Fig. 3). The average slant-height of these conical structures was 5 cm., with a perimeter of about 28.2 cm. and a convex surface, therefore, of about 70.50 sq. cm. From the adhering point of the nidosome, dotted lines, the capsules radiated to the periphery of the conical body. This radiation was not so regular in some as in others, yet there was a prevailing regularity in this respect. In Fig. 3, the arrangement of the capsules does not represent the prevailing regularity, as it was necessary to select an entire nidosome for photographing, most of the other having been broken. The capsules contained from 10 to 22 eggs (Figs. 4–6). The actual method of deposition has not been observed, but it is conjectured from the knowledge of the anatomy of the animal that the capsules are imbedded in the gelatinous mass as the nidosome is deposited. The mucous gland, which consists of (1) albuminous gland, (2) nidamental gland (Lang, 1896), is in *Melibe* in direct connec-

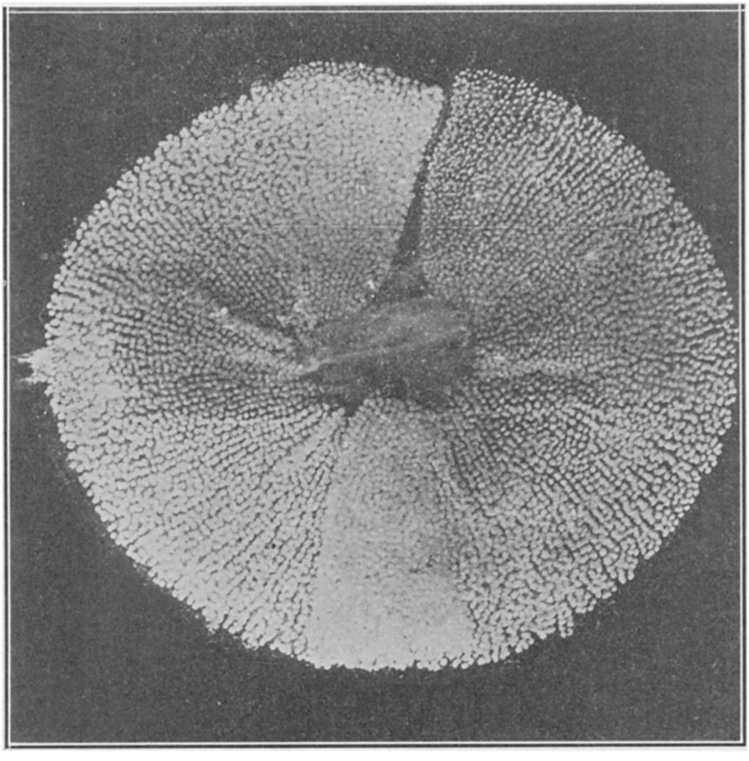

FIG. 3. Photograph of a nidosome of *M. leonina*, natural size. The dark band at right angle to the fold is a piece of eel-grass to which the egg-body is attached. The many radiating white dots are egg-capsules containing from 15–22 eggs.

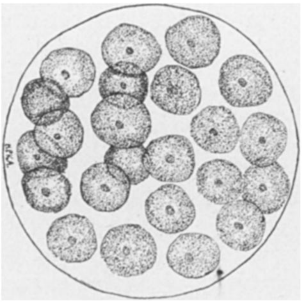

Fig. 4.

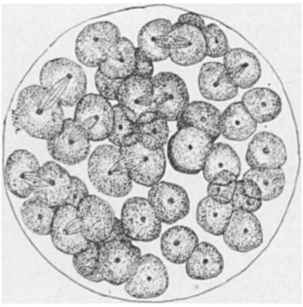

Fig. 5.

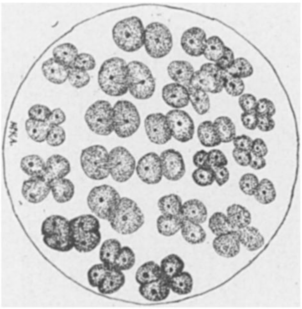

Fig. 6.

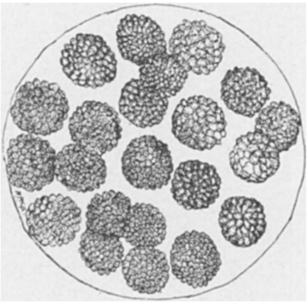

Fig. 7.

Figs. 4–7. Drawing of egg-capsules from a nidosome laid in captivity, showing a varying number of eggs. Figs. 5–6 show the eggs in two and four-cell stage, three hours after the nidosome was laid. In Fig. 7 cleavage has reached the blastula stage. The more oblong embryos are moving within the capsules.

tion with the vaginal orifice. In copulation, the penis, which is long, twisted like a screw, and of tough musculature, is inserted into the posterior genital pore of the mate, and so firm is the union that separation may not occur even though the couple be dipped from their natural abode and placed in a vessel.

Observations in the Laboratory

A study of *Melibe leonina* from an embryological standpoint, was made at the Biological Station. From the lot collected, some were preserved, others were kept alive in an aquarium. One morning, however, all save one were dead. Later, this one also seemed dead, and it was thought that the water had become stale. *Melibe* lay absolutely motionless on the bottom, all its muscles completely relaxed, and showed signs of life only after the water had been oxygenated for several minutes. It is muscular relaxation of this sort that *Melibe* assumes when it sinks from the surface to deeper water. After this the writer became used to its death feigning and needed only to oxygenate the water for it to become active again, crawl along the bottom and side of the aquarium, and after a while start swimming in the vessel. Changing of the water could not be done indefinitely, as on another morning a nidosome was found to have been deposited by the animal during the night. It was a funnel-shaped, transparent, gelatinous body adhering by the tapering end to the side of the jar. Viguier, 1898, when trying to prepare a specimen of *Tethys fimbriata* for fixation, observed the same phenomenon. He, however, did not change or oxygenate the water; he left the animal in it for about two weeks, when he found that an egg-body had been deposited, the eggs having ceased to divide in the four-cell stage. The nidosome of *T. fimbriata* is quite different in shape from that of *M. leonina.* In the case of *Melibe* the eggs continued to divide until they were transformed into larval forms, which actually turned the whole nidosome into a vibrating mass. The development continued, apparently normally, until the larvæ left the capsules, when they soon died. That the delicate molluskan young should die when coming in direct contact with the water of the aquarium was expected, as the renewing of the water was stopped after the nidosome was deposited, it being thought undesirable to disturb it too much; after the deposition of the egg-mass the water was simply kept at constant level, and oxygenated from day to day, so that the animal should not die. When the young *Melibes* were hatched the mother animal, without being further inseminated, laid another nidosome, which also hatched two weeks later. The eggs of the first nidosome developed into distinctly living creatures, moving about in the capsule on the fifth day after the setting (Fig. 7); it took two weeks for the complete development of the young. Alder and Hancock, 1845, p. 25, say:

> The embryo matures after deposition of spawn, from a few days to a month or more, according to species; the actual time appears to be about ten days or a fortnight.

Temperature, no doubt, plays an important part in the speed of development. Stuart, 1865, says:

> Gewöhnlich wird von den Opisthobranchiereiern angegeben, dass die Dauer der Entwickelung des Embryo ein Monat ist, in meinem Falle war sie circa zwei Monate; dabei war die vorherrschende Witterung, die für Sicilien jedenfalls eine kalte zu nennen war, gewiss von grossem Einflusse (p. 96).

The second nidosome was to some extent abnormal, compared with the first, and with those collected from the eelgrass. It showed a variation of the number of eggs in the capsules, from one to fifteen (Figs. 8–9). This abnormality was perhaps an indication of the decline in vitality of the mother animal. In fact, the adult specimen had greatly decreased in size since its capture.

One difficulty was that of keeping the water at a constant density. In order not to break the nidosome the water was only oxygenated and kept at a constant level. Each time when the eggs were examined, small portions of the nidosome were removed, and by so doing the membrane of the egg-body was broken. This did not seem to affect the development, however. Yet it was thought safer to keep the water at the same temperature as hitherto, than to change it daily, as the latter might cause too great physical shock. The abnormality of the water, as said, did not affect the embryos as long as they were within the capsules of the nidosome. Perhaps thus far in their development they were not affected by the abnormality of the water; even though the egg-body was punctured and broken in the examination of the eggs, the embryos seemed all to develop, as far as could be detected, and to pass through the normal developmental changes of a typical gasteropod.

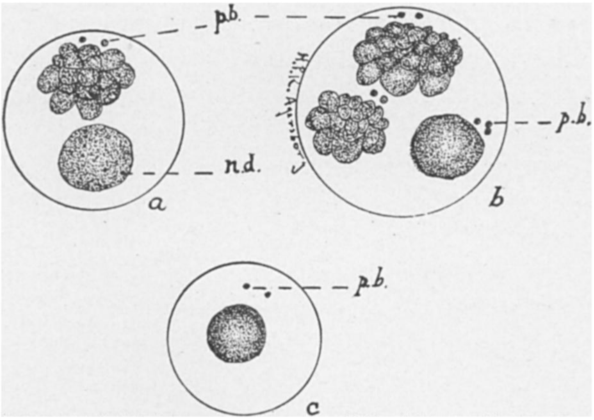

FIG. 8. Three abnormal egg-capsules from the second nidosome deposited after insemination; *a, nd.* no cleavage. *pb,* polar body; *b, pb.* first polar body has divided, but no cleavage in the egg; *c,* no cleavage of egg although the polar bodies were given off.

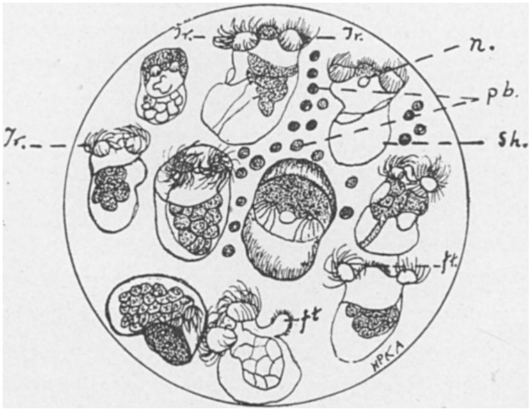

FIG. 9. An average sized capsule from the second setting after insemination; *n,* pedal ganglion; *ft,* foot; *pb,* polar body; *sh,* shell; *tr,* velum; all the embryos are in the veliger stage.

Abnormality in the second nidosome was marked by the reduced number of eggs within the capsules and in the early development in the eggs. The variation of the number of eggs in normal capsules was most marked at the end of the egg-belt. This abnormality was much greater in the second nidosome, in that there was a much greater number of small capsules with only one or a few eggs in them. There were also capsules actually without eggs. Some eggs failed to develop; some gave off the polar bodies and then did not advance any farther; others did not form polar bodies. It was of great interest, indeed, to watch the development of the embryos in the large capsules which in some cases contained more than twenty eggs (Fig. 7). Within a few hours, there would be twice or even three times as many polar bodies as eggs (of course within the capsules), because the first polar body sometimes divided. A detailed study of the blastomeres was not undertaken. Figures 4 to 6 show a few early developmental stages, and early and late larval stages are shown in Figs. 7 and 9. An embryonic shell is shown in Fig. 10; veliger larvæ in Fig. 9.

When the embryos reached the gastrula stage they swam about within the capsules. On the fifth day after being laid the whole egg-body was practically alive with imprisoned swimming larvæ (Fig. 9). Nine days later, the larvæ began to leave the capsules. It was surprising to see how rapidly the embryos advanced from day to day, going through the trochophore and veliger stages. During the latter stage the shell was very prominent; it resembled the shell of *Natica russa,* in that it had a blunt apex and short body; the posterior or tapering part of the shell had no spiral turns; the posterior edge of the aperture had a small indent; the edge of the aperture of the shell was otherwise without any modifications (Fig. 10). The animal itself did not assume the adult shape before it lost the shell, but when it left the capsule it shed the shell, and the young began the life of a so-called naked mollusk. The presence of a shell with operculum in embryonic life of Nudibranchs has been observed by various authors: Alder and Hancock, 1845; Pelseneer, 1893; Smith, Bell and Kirkpatrick, 1905; Boas, 1916, and others.

A large number of eggs were present in each capsule of the first nidosome (Figs. 4–7), and all developed into embryos which finally went through metamorphosis. In the second nidosome, some of the eggs failed to develop. The cause was perhaps lack of spermatozoa. During copulation, the spermatozoa become stored in the spermatotheca but also wander up the uterus as far as the prostate gland (Fig. 11, *spt.*, *ovd.*, *pr.*). The eggs are probably fertilized while passing down the uterus, *ut.*, or while in the spermatotheca, *spt.*, as many eggs actually pass into this out-pocketing of the uterus, the spermatotheca may therefore be termed ovo-spermatotheca. The only means of regulating the fertilization process in the egg must be the physical condition of the egg, which determines the reception or the function of the sperm; as all eggs, under natural conditions, contained in one and the same capsule, and, indeed, in the entire nidosome, go through simultaneous development, although they all (perhaps more than 100,000, in one normal deposit, nidosome) can not possibly have been fertilized at the same moment. This primary part of fertilization must take place before the eggs are incapsulated. If, however, an insufficient number of spermatozoa are present during the flow of the eggs, some eggs may become incapsulated without having been fertilized. One thing noted was

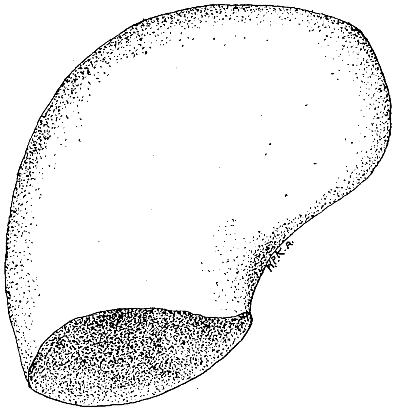

FIG. 10. Embryonic shell of *Melibe leonina.*

that the eggs in one end of the nidosomic belt, and in the main part of it, were all fertilized, while the other end (the last end) of the belt showed lack of fertilization. Another fact noted is that *Melibe leonina* carries over spermatozoa in its genital vessels; that more than one egg-body is deposited after insemination.

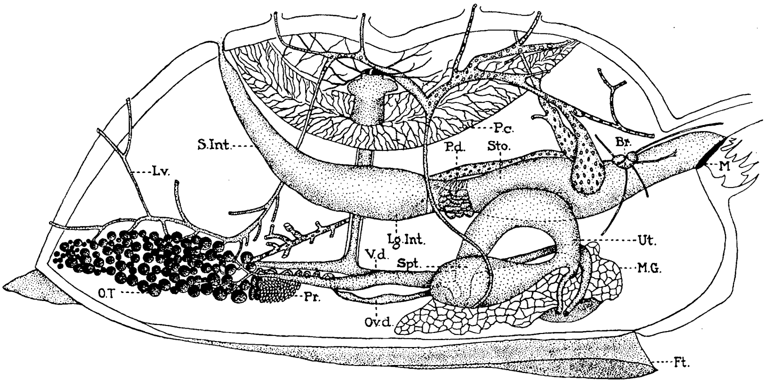

FIG. 11. Schematic drawing of dissected adult animal to show the general arrangement of the visceral organs: *Br*, brains; *Ft*, foot; *Lg. int*, anterior and large part of the intestine; *M*, mouth; *Mg*, mucous gland; *Ov. d*, oviduct; *Pc*, pericardium; *Pr*, prostate; *Si*, small part of the intestine; *Sto*, stomach; *Ut*, uterus; *Vd*, vas deferens; *Lv*, branch of liver; *Spt*, ovo-spermatotheca.

Reid's observations, 1846, on *Doris bilamellata, D. tuberculata, Gonidoris barvicensis, Polycera quadrilineata, Dendronotus arborescens, Doto coronata,* and a species of *Eolis,* bring out the same fact, viz., more than one deposit takes place after insemination. From 26 hours after coitus deposition may begin; "it does not, however, appear to be absolutely necessary for the production of fertile ova in all, if in any of the individuals of the nudibranchiate Mollusca, that coitus should have so shortly preceded spawning as was observed in Polycera, for an Eolis which was kept strictly confined in a vessel by itself, deposited, on the tenth and again on the thirty-second day of its isolation, abundance of fertile ova." Crozier, 1919, claims that the larger animals of *Chromodoris zebra* Heilprin, lay several more egg-masses in a given time than do small ones; that it is consequently of advantage to the species that large individuals should mate together; that there is, in fact, selective pairing which is of a distinctly advantageous or "purposeful" character, since it makes for the multiplication of the species. The same author, 1917*a,* records the unique findings relative to a rather high degree of correlation between the sizes of the two pairing members of *Chromodoris zebra.* The writer has observed the same fact relative to copulation among the Eolidæ. As for *Melibe leonina,* it is also true that those found copulating were of the same relative size. But even so, as seen in the second nidosome of *Melibe,* the animal may run short of spermatozoa during ova-deposition. To guard against this, there is, as shown by Crozier, among certain species, selective pairing between individuals of nearly the same size. Garstang, 1890, finds a considerable variation between the offspring of *Lomanotus* Vérany, "the individuals apparently showing a tendency to unite rather with those of their own variety than with those unlike themselves."

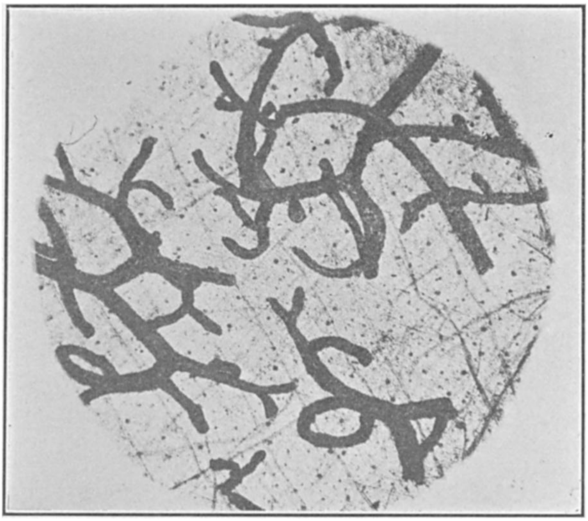

FIG. 12. Micro-photograph of the inner side of the ectoderm of the body-wall, showing the odoriferous glands, the small dots among the branching (black) hepatic cæca, and the crossing muscle (pale) fibers.

To understand the process of insemination of the eggs, and the conditions controlling the number of eggs in the capsule, a little speculation is necessary. It seems as if the processes of fertilization and incapsulation are effected during the emission of the eggs; that when the eggs pass down the uterus or pass the spermatotheca they are fertilized, and immediately after that incapsulated, and that the size of the capsules and the number of eggs present in each capsule are regulated by the speed of the outflow of the eggs. The size of the capsule, as a rule, varies according to the number of the eggs present within the capsule. It seems puzzling, however, when capsules are found without eggs, and with eggs which show no indication of being fertilized, but this abnormality is limited to the last part of the nidosomic belt, and is of course so controlled that an entire egg-body may not be deposited without some eggs at least being present, and being fertilized. It is a matter for future observation to determine whether individuals in ova-maturity are capable of depositing normal nidosomes, without being stimulated by an individual in ripe male-phase. It is a question whether the mere pressure of ripening eggs will cause egg-flow. Crozier, 1917*b*, reports, however, that *Chromodoris zebra,* if left alone, deposits fragments of egg-bodies which are not fertilized. The writer has noted the same phenomenon relative to *Eolis olivacea* when it is kept alone; but also in this case, as in the case of *Chromodoris,* no normal nidosomes were deposited.

The question of cross-fertilization becomes of interest since spermatozoa are found in both genital ducts of the same individual, from the ampulla of the penis and all the way down the penis to the end of it; from and including the prostate which surrounds the uterus, to and including the ovo-spermatotheca. If self-fertilization takes place, should there be any shortage of spermatozoa during ova-deposition? The presence of spermatozoa in the female genital tube is undoubtedly the result of coition and the wandering of the spermatozoa up the uterus, against the outward current of that organ. Alder and Hancock, 1845, p. 25, say:

> The Nudibranchs, notwithstanding that they are androgynous, frequently copulate during the breeding season. The conjoined individuals lie side by side, their heads turned in opposite directions. Thus the right sides of the two animals are brought in close contact, and mutual impregnation is effected. They remain in this position for some time, but in a short period after separating, generally about the first or second day, the spawn is deposited.

Crozier, 1919, claims that *Chromodoris zebra* is functionally hermaphroditic, and effective reciprocal insemination is practised. But this is not practised among the species *Melibe leonina;* although semen may be present at the same time in both genital ducts, insemination is not reciprocated simultaneously. That is, in all the individuals examined, coitus was effected by the introduction of the penis of the one mate; the penis of the other mate was completely withdrawn. Whether spermatozoa were present in the members whose external genital organs were not visible was not determined. It looks, however, as if *Melibe leonina* is protandric, a condition, according to Pelseneer, 1895, common among *Eolis, Elysia,* and *Clione limocina.* Eliot, 1910, says:

> Pairing, according to Hecht, is reciprocal, and though hermaphrodite Mollusca are incapable of self-impregnation both individuals spawn after mating.

The writer has observed on *Eolis olivacea,* at Woods Hole, that one mate may start spawning while copulating. Spermatozoa, according to Reid, may be carried in the female genitals (*Eolis*) for more than thirty days before being used. That is, cleavage does not start in the eggs of *Eolis* until after deposition; fertilization, therefore, may not occur before the time of incapsulation. Spermatozoa are kept alive in, and stimulated by, secretions of the female genital organs, as shown by Eliot and Evans, 1908, p. 287:

The walls of the spermatotheca (of *Doridoides gardineri*) are thick and produce a secretion. In some specimens small clumps of spermatoza are embedded in this secretion. In others all the spermatozoa form a central mass in the main cavity of the spermatotheca. It is possible that the secretion serves to form small packets of spermatozoa or spermatophores.

Summary

1. *Melibe leonina* is a large carnivorous Nudibranch reaching sometimes 14 centimeters in total length; it is an actively predaceous animal; it practically gorges itself, feeding mainly on small Crustacea; it is gregarious.
2. It seems to live more than one year; its recurrence is spasmodic.
3. It swims freely in the water, backward, upward or downward; it crawls on the surface by the surface tension, and on sea-weeds, by the help of its highly ciliated foot.
4. Its defensive means are an offensive odor and death feigning.
5. It drops to deeper water by relaxation of its muscles.
6. It collects in groups among sea-weeds, where copulation takes place.
7. Mutual insemination does not seem to be simultaneous.
8. It spawns as early as March and as late as July; sexual maturity is reached quite early, as young ones two centimeters long were found with ripe spermatozoa.
9. Spermatozoa from another individual are stored in the ovo-spermatotheca but wander up the uterus as far as the prostate.
10. Eggs are also stored in the spermatotheca, hence the name ovo-spermatotheca.
11. Copulating individuals are of the same relative size.
12. The same individual deposits more than one nidosome, after insemination; spermatozoa may be carried over in the ovo-spermatotheca at least two weeks.

13. The eggs are deposited in capsules, normally containing from 15 to 22 eggs. The capsules are arranged in rows within a gelatinous mass, sometimes quite regularly; the gelatinous mass is formed into a belt from 3 to 5 cm. wide; the mucous flow is greater in one side of the belt than in the other, so that one side of the belt is shorter than the other, and the belt curves into a funnel-shaped mass, the apex adhering to some sea-weed, near the surface of the water.

14. Eggs may become incapsulated without being fertilized; no cleavage of such eggs follows.

15. Normally the embryo develops within two weeks.

Acknowledgment

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